

*Anim. Behav.*, 1976, 24, 354-363

## A SOCIAL ETHOGRAM OF THE NEOTROPICAL ARBOREAL ANT *ZACRYPTOCERUS VARIANS* (FR. SMITH)

By EDWARD O. WILSON

*Museum of Comparative Zoology Laboratories, Harvard University, Cambridge, Massachusetts 02138*

**Abstract.** An ethogram is presented of *Zacryptocerus varians*, a morphologically advanced member of the 'turtle ants' comprising the neotropical ant tribe Cephalotini. The species displays unusual and in one or two cases possibly even unique social behaviours, including the consumption and sharing of infrabuccal pellets, the apparent absence of adult transport, a primarily or exclusively mechanical form of colony defence, and a remarkable form of abdominal trophallaxis. All of these specializations seem to be associated with more primary adaptations by the species to arboreal nesting and scavenging. Among the additional results is the demonstration that the major worker is more specialized as a defensive caste than is the case in certain species of *Camponotus* and *Pheidole*.

The ethogram, or complete catalogue of the behavioural patterns of a species, is a far more practicable goal in the case of social insects than it is in vertebrates. Wilson & Fagen (1974), in an analysis of the ant *Leptothorax curvispinosus* Mayr, estimated that twenty-seven categories of interactions, which were obtained with only 1962 observations of behavioural acts spread over an accumulated period of 51 hr, covered no less than 77 per cent of the total social repertory displayed within and in the immediate vicinity of the nest. More precisely, it was estimated that the total number of categories of interaction, examples of which include grooming larvae, carrying dead nestmates, stridulating, and so forth, is twenty-nine, with a 95 per cent confidence interval of [27, 35]. The sample coverage, which is the estimated probability that each new act will fall in a category already seen, was a much higher value, 0.9995. These levels were reached in *Leptothorax curvispinosus* much more quickly than in mammals because of two features of ant behaviour: the smaller repertory of the ants and the smaller proportion of their behavioural categories that are relatively rare in occurrence.

Ant behaviour can thereby be encompassed more readily than vertebrate behaviour. Moreover, the colonies can be studied under laboratory conditions that facilitate experimentation and the recording of data. Entire colonies of many species can be placed on the stage of a dissecting microscope or within the field of a motion-picture camera and all their members monitored simultaneously. Myrmecologists are consequently in a position to proceed with comparative sociobiology at a quick pace. Why

they have not done so until now can be explained by two historical circumstances: the lack of understanding of the true basis of communication in ants, and the failure to appreciate the advantage intrinsic in the relatively sparse social repertories of these insects. Both difficulties having recently been remedied (see reviews in Wilson 1971; Hölldobler 1976), we can proceed with the systematic exploration of the approximately 270 genera and 12 000 species of ants. Only through ethograms, organized in a way that permits species and even genera and tribes to be closely compared, will it be possible to trace social evolution efficiently within the ants as a whole. In ordinary reports valuable data can be and are presented within the contexts of narrow experimental design, but this format causes whole categories of behaviour to be overlooked, and other useful observations noted fortuitously outside the scope of the experiments are seldom recorded.

The present report comprises an example of social ethogram mapping in ants. Earlier efforts have included the analysis of *Leptothorax* just cited plus an earlier, non-quantitative study of *Daceton armigerum* (Wilson 1962). The importance of the species considered here, *Zacryptocerus varians*, is threefold. It is an advanced member of one of the least known major ant tribes, the Cephalotini; and it is extremely modified for an arboreal existence, offering the opportunity to study the influence of this adaptation in the modification of the basic ant social system. Finally, *Z. varians* has one of the most extreme and bizarre physical caste systems, and for this reason it was selected to be included in the author's current study of ant castes.

### The Ant Tribe Cephalotini

The myrmicine ant tribe Cephalotini is an exclusively arboricolous New World assemblage containing approximately 110 species (Kempf 1951, 1958, 1963, 1964, 1973). So far as known, all of the species are distinguished from all other ants by the peculiar mushroom-like structure of their proventriculus. The external appearance and defensive behaviour of most of the advanced species would seem to justify referring to the cephalotines by the convenient vernacular name 'turtle-ants'. In his latest conspectus, Kempf recognized the following four genera: *Procryptocerus* Emery (thirty-four species); *Cephalotes* Latreille (four species); *Eucryptocerus* Kempf (four species); *Zacryptocerus* Wheeler (seventy species; = *Paracryptocerus* Emery, = *Hypocryptocerus* Wheeler).

*Zacryptocerus* is the largest, geographically most widespread and most diverse of the genera. It also contains the anatomically most modified forms. Several behavioural studies have previously been conducted on *Zacryptocerus*. Coyle (1966) demonstrated the existence of two alternative defensive techniques among various Central American species: some species emit a volatile chemical secretion from the tip of the abdomen, which can be tipped forward over the thorax due to lowering and flattening of the propodeal and petiolar dorsa. Others rely on heavy spine formation and quick movements for defence. Creighton and his co-workers (Creighton & Gregg 1954; Creighton 1963; Creighton & Nutting 1965; Creighton 1967) studied *Z. rohweri* and *Z. texanus*, which occur in the extreme south-western United States. They established the fact, which had been suspected by previous authors but not adequately proved, that the soldiers and queen use their shield-shaped heads to block the narrow nest entrances and even to 'bulldoze' opponents out of the nest passageways. Creighton et al. also discovered that the two *Zacryptocerus* collect certain types of pollen, in addition to aphid honeydew and crushed insect tissue, and are able to survive and reproduce on this food item alone. So far as is known pollen feeding is still unique to these ants. No evidence has yet been found of its occurrence in other kinds of ants, including the cephalotines *Cephalotes atratus* (Mary Corn, personal communication) and *Z. varians*.

**The Natural History of *Zacryptocerus varians***  
*Zacryptocerus varians* ranges from the tip of southern Florida, including the Florida Keys,

to the Bahamas, Cuba and Jamaica. It appears to be a West Indian species that has just managed to colonize the most tropical portion of Florida, and it is the only cephalotine known from the eastern United States. *Z. varians* has been found nesting in dead branches of a variety of trees, including *Bauhinia*, the sea grape *Coccoloba*, and (especially in the Florida Keys) the red mangrove *Rhizophora mangle*. Colonies have also been found in stems of tall grasses and sedges, including sea oat (*Uniola paniculata*) and saw grass (*Cladium jamaicensis*). In southern Florida winged forms have been encountered in the nests during the summer months of June and July. The author's experience in the field in Cuba and Florida indicates that the species is exclusively nocturnal in nature. However, workers come to forage both during the day and night under conditions of constant illumination in the laboratory.

'Mature' colonies, that is, colonies large enough to produce winged queens, normally contain from one to several hundred workers and soldiers. Although I have dissected many nests without encountering any mother queen, large numbers of nests have been opened containing a single mother queen, and none has contained more than one such individual. Consequently *Z. varians* can be assumed to be normally monogynous. The queen also appears to be essential for the production of new workers and soldiers. While queenright colonies in the laboratory produced large broods of these castes, queenless colonies reared under identical conditions produced only males, or no brood at all. Although exact censuses of colonies freshly collected in the field have not been made, the ratio of adult minor workers to soldiers is approximately 10:1, a proportion that is maintained in the laboratory (see Fig. 1). Colonies are discrete entities. When workers from one colony are introduced into the nests of another in the laboratory, they are attacked and driven out.

The diet of free-living colonies of *Zacryptocerus varians* is not known, but it can be partly inferred from laboratory studies. In the laboratory the foraging minor workers are totally inept as predators. When workers encounter live insects outside the nest they generally avoid them. The very short mandibles and rigid body form make them physically less capable of pursuing prey even if the behaviour were well developed. Even small aphid nymphs just large enough to fit between the mandibles of the ants

were handled ineptly in laboratory tests. The *Zacryptocerus* pushed at the aphids with their heads, seized and carried them briefly in their mandibles and then, invariably, broke contact and ran away. Not a single aphid was carried back into the nests. It is a remarkable fact that no solid food of any kind was ever seen to be carried into the nests, although the ants were presented with abundant quantities of diverse materials over a period of months. The ants are nevertheless strongly attracted to the tissues and haemolymph of freshly killed insects. This material they scrape, lick, and nibble away, swallowing all that they acquire and later regurgitating the liquid or semiliquid food to their nestmates. All of the insects offered in this manner were accepted: cockroaches, a nymphal chermid, two species of scarabaeid beetles, tachinid and muscid flies, a geometrid moth, and a variety of microlepidopteran moths. On four occasions workers were observed feeding on one of their own larvae. The workers prefer freshly killed insects to decomposed ones. Although fragments of insects in all stages of decomposition were available in the nest vicinity, and occasionally in abundance, foragers were seen to lick them on only two occasions, and then only for a few minutes. Honey and sugar water were avidly accepted by laboratory colonies. Also, natural honeydew was taken when leaves containing aphid colonies were placed near the nests. The possibility that *Zacryptocerus varians* feeds on pollen has not been adequately investigated. Workers offered pollen from tiger lilies (*Lilium tigrinum*) showed an interest in this material, but did not carry it into the nest or consume it, as do workers of *Z. rohweri* and *Z. texanus* when presented other species of pollen. It is conceivable that *Z. varians* will feed on certain kinds of pollen. But if it does, this item is not essential. In the laboratory, colonies flourish on a diet of fresh insects and honey. In the red mangrove forests of the Florida Keys, where pollen is very scarce during most of the year, *Z. varians* is one of the most abundant ants.

In short, *Z. varians* is a scavenger. The full extent of its diet can be worked out only by field studies, but it is clear that the species will accept a wide range of fresh insect materials. It appears to have surrendered all attempts at predation. This concession is in concert with its passive form of defensive behaviour, to be characterized later.

### Methods

The colonies of *Z. varians* used in the present study were collected from dead stems of red mangrove in the central Florida Keys. They were forced to move into glass tubes 10 cm long with internal diameters of either 2 or 3 mm, plugged at one end with cork disks or cotton plugs and left open at the other end to permit the ants to forage outside. Each set of tubes containing a colony was placed on the floor of a glass finger bowl 20 cm in diameter and 8 cm deep, small enough to be fitted onto the stage of a dissecting microscope. As a consequence, the entire populations of the colonies, which contained less than one hundred adult individuals, could be monitored simultaneously. It was possible to record nearly all of the discrete behavioural acts of every member of the colony. During a period of 6 weeks, a total of 25.5 hr were devoted to two colonies and 2542 separate behavioural acts recorded. The observation hours ranged casually from 9.00 hours through the day and first part of the evening to past 24.00 hours; during this span of time no differences in level or patterns of activity were noted. The colonies were maintained on daily feedings of insect fragments and honey. Most observations were made at magnifications between 10 $\times$  and 28 $\times$ .

Voucher specimens have been deposited in the Museum of Comparative Zoology, Harvard University.

### Results

The behavioural catalogue of the more intensively studied of the two colonies, incorporating the social ethogram, is presented in Table I. Thirty-eight categories of behavioural acts were recorded in the minor worker caste. When the frequency data (number of acts observed per category) were fitted to a lognormal Poisson distribution by the Fagen-Goldman method (see Fagen 1974), the total number of behavioural categories, including those still unseen, was estimated to be forty-two, with a 95 per cent confidence interval of [38, 46]. The catalogue of the second, less thoroughly studied colony did not differ significantly and will not be presented. In the following sections a more detailed account will be given of those traits in which *Zacryptocerus varians* differs from other ants, or at least most other ants. Then in the Discussion, the ecological, significance of these peculiarities will be considered.

**Antennal tipping.** This is the term I have applied (Wilson & Fagen 1974; Wilson 1975)

Table I. Relative Frequencies of Behavioural Acts by the Three Female Castes in a Single Colony of the Ant *Zacryptocerus varians*. (N, Total Number of Behavioural Acts Recorded for Each Caste). Nest Population = One Nest Queen, Sixty-Six Minor Workers, Seven Major Workers, Seven Eggs, Fifty-Eight Larvae, Two Pupae

Behavioural act	Minor workers (N = 2163)	Major workers (soldiers) (N = 61)	Queen (N = 7)
1. Self-grooming	0.2621	0.3443	0
2. Antennal tipping: tips of antennae brought together as body is held rigid	0.0009	0	0
3. Allogroom minor worker	0.0467	0.0656	0
4. Allogroom major worker	0.0028	0	0
5. Allogroom queen	0.0023	0	0
BROOD CARE			
6. Carry or manipulate egg (or eggs in succession)	0.0065	0	0
7. Lick egg (or eggs in succession)	0.0074	0	0
8. Carry or manipulate larvae (or larvae in succession)	0.0518	0.0328	0
9. Lick larvae (or larvae in succession)	0.1188	0.0328	0
10. Assist larval ecdysis	0.0005	0	0
11. Assist ecdysis to pupa	0.0032	0	0
12. Carry or manipulate pupa (or pupae in succession)	0.0055	0	0
13. Lick pupa (or pupae in succession)	0.0079	0.0328	0
14. Assist eclosion to adult	0.0009	0	0
15. Lay normal egg	0	0	0.1429
REGURGITATE			
16. With larva	0.0536	0.0492	0
17. With minor worker	0.2164	0.2951	0.8571
18. With major worker	0.0083	0.0656	0
19. With queen	0.0028	0	0
ABDOMINAL TROPHALLAXIS			
20. Receive or solicit from anal region of minor worker	0.0125	0	0
21. Receive or solicit from anal region of major worker	0.0032	0	0
22. Receive or solicit from anal region of queen	0.0028	0.0164	0
23. Lick wall of nest	0.0060	0.0492	0
24. Forage outside nest	0.0698	0	0
25. Feed on honey outside nest	0.0411	0	0
26. Feed on solid food (trophic egg, larval skin, etc.) inside nest	0.0079	0	0
27. Feed on insect outside nest	0.0171	0	0

28. Carry dead insect	0.0046	0	0
29. Carry dead nestmate	0.0129	0	0
30. Carry live adult nestmate	0	0	0
31. Extrude sting and/or anal tube	0.0023	0	0
32. Lay odour trail to food	0.0023	0	0
33. 'Jittering': vibrating entire body up and down	0.0028	0.0164	0
34. Extrude infrabuccal pellet	0.0014	0	0
35. Feed infrabuccal pellet to larva	0.0018	0	0
36. Lay trophic egg	0.0023	0	0
37. Feed trophic egg to larva	0.0032	0	0
38. Feed trophic egg to minor worker	0.0005	0	0
39. Cannibalism: feeding on own larva	0.0009	0	0
40. Excavating	0.0060	0	0
	1.0	1.0	1.0

to the following strange behaviour observed in certain myrmicine ants: the body is held rigid (sometimes it quivers slightly and is raised by an extension of the legs) and the antennae are held with the tips pointing toward each other and occasionally even touching. The behaviour has been observed in workers of *Pogonomyrmex badius* and *Leptothorax curvispinosus*; Mary Corn (personal communication) has also seen it in *Cephalotes atratus*. The significance of antennal tipping remains unknown.

**Jittering.** Both minor and major workers were occasionally observed to vibrate their entire bodies in a mostly vertical plane through light but rapid pumping of the legs. Once a minor worker vibrated the fore part of the body steadily while occasionally bringing the abdomen into play as well. In most instances the behaviour, which I have labelled jittering, was accompanied by the licking of another adult or larva or the regurgitating to it. Jittering did not resemble stridulation, and nestmates in the vicinity showed no visible response to it.

**Regurgitation.** The rate at which the minor workers regurgitate liquid back and forth is exceptionally high for ants, especially for myrmicines. For example, regurgitation with other adults made up 22.8 per cent of all behavioural acts in *Z. varians* minor workers, as opposed to only 7.8 per cent in workers of *Leptothorax curvispinosus*, and was wholly absent in *Pogonomyrmex badius*. This higher frequency apparently reflects the exclusively liquid or semiliquid diet of the *Zacryptocerus*.

In fact, no solid materials are brought into the nest.

**Abdominal trophallaxis.** So far as is known the behaviour now to be described is unique within the ants; it has not been observed even in *Cephalotes atratus*, the second member of the Cephalotini under intensive study (Mary Corn, personal communication). In abdominal trophallaxis the soliciting ant behaves in a fashion seemingly identical to that in oral trophallaxis, but the orientation is different: the worker holds her mouthparts precisely to the tip of the abdomen of the 'donor' ant (where the hindgut, ovaries and sting all exit), while licking the tip with her glossa and vigorously but lightly stroking the area immediately surrounding the tip with her antennal funiculi and occasionally her fore tarsi also. The behaviour is strongly different from ordinary allogrooming, in which the tip of the abdomen is licked only in passing as the allogroomer covers all parts of the abdomen. Also, in ordinary allogrooming the soliciting movements of the antennae and fore tarsi are never seen. Occasional workers display a 'hunger' for whatever material they receive from the abdominal tip; such individuals move from one nestmate to another while soliciting in the trophalactic manner. The attempts appear either to fail completely, in which case contact is broken off quickly, or to succeed sufficiently for contact to be sustained much longer. Thus five typical contacts timed between minor workers had the following durations: 1, 1, 1, 24 and 55 s. Four contacts in which minor workers approached major workers were timed as follows: 2, 2, 13 and 53 s. The donor ants often respond co-operatively to the touch of the solicitor, lifting the abdomen in the direction of the solicitor's head. Also, donors can occasionally be seen to 'call' solicitors by lifting the abdomen, extruding the anal or sting regions, or both. In one extreme example, a minor worker was observed to extrude its abdominal tip repeatedly over a period of at least 15 min, at intervals of about thirty seconds. First, the terminal five segments of the abdomen (those following the very large anterior segment of the gaster) were extended out slightly. Then the sting and anal tube were extruded, exposing the glistening membranes around these organs. No less than five other minor workers approached in succession during these episodes, antennating and licking the abdominal tip in the manner previously described.

What are the attractive materials? On several occasions I saw the solicitor ants licking what appeared to be a film of liquid at the abdominal tip, but I could not be sure. Also, there was no direct way of ascertaining the source of the attractant. Hence the provisional use of the imprecise expression abdominal trophallaxis is suggested rather than ovarian trophallaxis, anal trophallaxis, or whatever. Even so, some indirect evidence exists that the attractant may in fact be at least partly ovarian in origin. Workers are strongly attracted to the trophic eggs laid by nestmates, and they eat them on occasion, therefore competing with the larvae for this rich foodstuff. On one occasion, a minor worker was observed to lick the film of liquid remaining on the nest floor after a trophic egg had been laid and removed intact. Hence the surface fluids of the eggs are attractive. Still more significantly, a worker was observed to be solicited by two workers immediately after it had laid a trophic egg and while it was still feeding the egg to a larva.

In further support of the ovarian-attractant hypothesis is the fact that *Zacryptocerus* workers do not depend on nestmates to remove their anal material. Like other ants, the *Zacryptocerus* deposit faecal smears on the floor of the foraging area outside the nest. Neither their arboreal habits nor rigid body form has interfered with this basic function.

As stated, abdominal trophallaxis of the kind reported here does not appear to have been seen in other kinds of ants. *Myrmecia gulosa* workers sometimes solicit trophic eggs from one another, but not by direct begging from the abdomen. Freeland (1958) describes the process as follows: 'During winter, though larvae were not known to be fed with eggs, workers (except in the coldest weather) frequently solicited eggs from other workers and ate them: a worker would approach another and, placing its mandibles above those of the potential donor, begin plying its mandibular tips with the palps, simultaneously tapping or stroking it about the head with the antennae. The passive worker, after a variable period of such stimulation would begin flexing its gaster ventrally, more or less rhythmically, until it was curved well forward under the thorax. The egg material began to emerge and was taken, often before it completed its passage, by the soliciting worker, or sometimes by a third individual.' No solicitation of any kind was observed by the same author in *Myrmecia forceps*. However, a similar

pattern of head-on solicitation has been observed in *Dolichoderus quadripunctatus* by Torossian (1959). Both queens and workers use the method to obtain eggs from other workers.

**Normal and trophic eggs.** The 'normal' eggs of the queenright colony, i.e. those destined to hatch into larvae instead of being eaten, are probably laid by the queen. The evidence for this conclusion is indirect: in queenright laboratory colonies the eggs always developed into minor and major workers, suggesting that they had been fertilized; whereas queenless colonies either did not produce viable eggs, or else the eggs always developed into males, suggesting that they were unfertilized. As illustrated in Fig. 1, the eggs are very large. Most are 1.1 to 1.2 mm in length, one-quarter or more as long as the queen's abdomen. The rate at which these eggs are laid must also be exceptionally low, because I failed to see a single instance of oviposition in 25.5 hr of observing two queenright colonies. The phenomenon is similar to that noted by Michener (1973) in allodapine bees, in which large egg size is associated with low oviposition rate. Michener notes that small egg size permits the deposit of eggs in batches, so that the brood tends to develop synchronously and can presumably be handled with greater efficiency by the nurse workers. This conclusion is reasonable but does not explain why the eggs of some species are large. The reason in both the allodapines and *Zacryptocerus* ants may be that larger size reduces the rate at which eggs lose moisture,

an adaptation to the dry arboreal nest sites favoured by both the bees and ants.

Trophic eggs are laid by minor workers. It is possible that they are also laid by major workers, even though such oviposition was not seen in this caste, the reason being that major workers comprise such a small percentage of the adult population that the behaviour might have been simply a statistically unlikely event during the cumulative observation period. Major workers, like minor workers, have well-developed ovaries, even in queenright colonies. Trophic eggs laid by minor workers are small, round objects with diameters only about one-fifth the length of the viable (queen-laid?) eggs. They are soft, tend to flatten from their own weight when placed on the nest floor, and are easily punctured. The minor workers, being unable to bend their abdomens forward in the usual manner of ants, hold their bodies straight and deposit the eggs on the nest floor. The laying worker then backs up, seizes the egg in its mandibles, and excitedly seeks the larvae. It thrusts the egg down onto the head of the first larva encountered and, if the larva reacts, holds the egg in place until it is mostly or entirely consumed. If the larva does not respond, the worker lifts the egg up and places it on the head of a second larva, continuing the process until a willing recipient is encountered.

**Fate of infrabuccal pellets.** Very little has been reported concerning the disposal by ants of infrabuccal pellets, which are the compacted pellets of solid material eaten but not passed

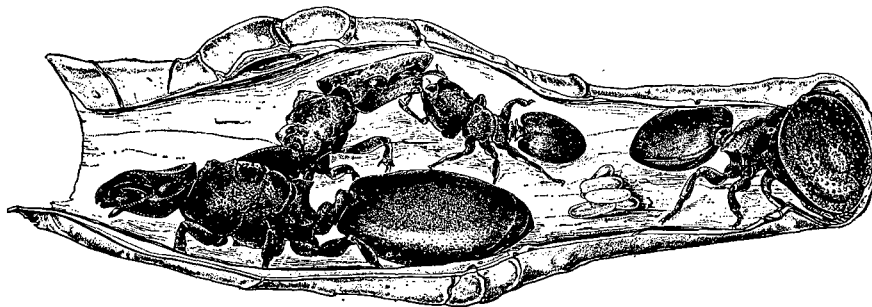


Fig. 1. The three female castes of the ant *Zacryptocerus varians* are included in this colony fragment, which occupies a typical nest cavity in a dead stem of the red mangrove, *Rhizophora mangle*. The nest queen rests on the floor of the cavity to the left, while on the right a large major worker blocks the nest entrance with its saucer-shaped head (an eye and an antenna can be seen just beneath the left margin of the expanded, circular frontal lobes). To the rear of the queen another major worker receives regurgitated liquid from a minor worker. (Drawing by Turid Hölldobler.)

to the crop. On one occasion I saw a minor worker 'cough up' such a pellet and immediately place it on the head of a larva, holding it in place for about two minutes. Then it pulled the object away and licked it for a minute longer, during which time the pellet diminished somewhat in size. Other pellets were observed on several occasions while being held in place on the heads of larvae or in the process of being partially consumed by workers. But this is not the invariable fate of the pellets. In one case I saw a worker discharge a pellet and proceed immediately to the nest entrance, where the object was dropped onto the floor of the foraging arena. Wheeler & Bailey (1920) observed workers of the arboreal ant genus *Pseudomyrmex* feeding infrabuccal pellets to larvae, while R. R. Snelling (personal communication) has recorded an instance of the same behaviour in *Camponotus rasilis*. I suggest that this behaviour, which so far has been seen only in arboreal ants, is a device used primarily for the conservation of water.

**Meconium removal.** On a single occasion, in the second of the two colonies monitored, the removal of a prepupal meconium was witnessed. There is no reason to believe that the act is exceptional for ants, but it has been so seldom noted in the literature as to deserve mention here. Two minor workers were observed to pull a large, black, spindle-shaped meconium from the hindgut of a minor-worker prepupa. As it emerged, they licked the meconium vigorously, and other minor workers occasionally joined them in licking but not pulling the object. The meconium evidently lost liquid by this action, because it shrank somewhat in size. However, no solid material appeared to be taken from it. After it was pulled free, the meconium was passed along the nest tube from one ant to the next. Eventually, 10 min 17 s after it was seen to be in an early stage of emergence from the prepupa, the meconium was deposited outside the nest 5 cm from the entrance.

**Cannibalism and necrophoresis.** On four occasions I saw dead larvae being consumed by minor workers. One of the corpses was also placed on the head of a live larva for a short time. The cause of death of the larvae was not ascertained. Dead adult *Zacryptocerus*, in contrast, were never consumed; their bodies were carried away from the vicinity of the nest and discarded.

**Recruitment.** The recruitment of nestmates has never been recorded previously in the

cephalotine ants. I evoked it repeatedly in *Zacryptocerus varians* by depriving laboratory colonies of honey for several days to a week and then providing them with a sizeable droplet outside the nest. The first minor workers to encounter the bait fed extensively on it, then returned to the nests dragging the tips of their abdomens over the floor of the foraging arena. Nestmates encountered were able to follow the trails outward for at least 10 cm and without further assistance from the recruiter. The trails remained active for only a few minutes. Furthermore, no evidence of orientation along persistent trunk trails was detected, even when long-lasting food sources were left in the foraging arena. Therefore the trail pheromone appears to serve primarily if not entirely for recruitment. It was possible to draw workers from the nest tubes using artificial trails drawn with crushed poison and Dufour's glands; following was nearly perfect for distances as great as 25 cm. The method was not precise enough to determine which of the two glands contained the trail pheromone. These artificial trails, like the natural ones, were short-lived.

**Adult transport.** It is a remarkable fact that no instance of adult transport was ever observed in the laboratory colonies, even on the numerous occasions when the colonies were spilled out into the foraging arenas and thus forced to find their way back into the nest tubes.

**Defence.** The conventional view of poly-morphic ants generally, and of cephalotines in particular, is that the major worker caste responds most vigorously to intrusions of the nest. *Zacryptocerus* majors have been considered to fill their main function simply by blocking the nest galleries and pushing intruders out of the nest entrances. But this is only a small part of the story. In fact, both minor and major workers of *Z. varians* proved to be very active. The minor workers have a lower response threshold, forming the 'early warning system' of the colony and disposing of minor intruders. Majors respond less readily, but once activated are individually more effective. The defence responses of the colony as a whole can be conveniently classified into two levels according to intensity:

(1) Low Intensity. The minor workers seize the intruder and drag or carry it out of the nest. The major workers may investigate briefly but do not otherwise participate. This is the form of response shown toward alien *Zacryptocerus* minor workers (and a worker of the tiny,

inoffensive ant *Strumigenys louisianae*) placed in the nest cavities.

(2) High Intensity. Both castes participate. The minor workers seize the intruder, usually by its appendages, and try to carry or to drag it from the nest. They also join the major workers in pushing the invader with their heads and in pinning it to the nest wall by pressing against it with their backs with legs extended. If these techniques do not work, numerous individuals of both subcastes gather around and form a solid plug, trapping the enemy; then, by squeezing and shoving, they gradually force it to the entrance and out of the nest. The major workers are the more effective in this mode of defence. Using its great saucer-shaped head (see Fig. 1) as though it were the blade of a bulldozer, one individual can block and push as effectively as two or more minor workers. Also, the major workers are more persistent once they have been activated, so that they become more heavily concentrated at the site of disturbance. The high intensity mode of defence was elicited in the laboratory by introducing workers of *Tetramorium caespitum*, which are approximately the same size as the *Zacryptocerus* minor workers, and by pushing dissecting needles into the midst of groups of workers.

Curiously, the *Zacryptocerus* showed no signs of using their stings, which are small but well developed. Nor was there any evidence of the employment of chemical defence, although the Dufour's and poison glands are typical in size for myrmicine ants and apparently normally developed. Intruders ejected from the nests invariably were able to walk away unharmed.

**Behaviour of the major workers and queens.** The major workers are very lethargic on almost all occasions except when defending the nest. Unlike the soldiers of *Camponotus (Colobopsis) fraxinicola* and *Pheidole dentata* (Wilson 1974 and unpublished), they are no more effective than minor workers in storing liquid food. This fact was ascertained by depriving a colony of honey for a period of 1 week, weighing a sample of ten minor workers and all of the six major workers, then feeding the colony to satiation for 2 days and weighing again. The average weight gain of the minor workers was 28.8 per cent, while that of the major workers was only 18.3 per cent, essentially the reverse of the situation in *C. fraxinicola*.

The *Zacryptocerus varians* major workers appear to function primarily in defence, and they deserve the title of soldiers. Yet they are

not wholly defensive automata. As indicated in Table I, the major workers sometimes wash and manipulate larvae and pupae. When the nest is broken open and the brood spilled out in the open air, the major workers join the minor workers in retrieving the immature forms. However, they are less effective in this role and retire more quickly to the interior of the nest.

The queens are even less active than the major workers. They are more sluggish than the queens of any ant species I have studied, standing immobile for long periods of time.

Both the major workers and the queens appear to live exclusively by liquid food regurgitated to them by the minor workers.

### Discussion

The six most distinctive features of the socio-biology of *Zacryptocerus varians* are listed in Fig. 2, and the inferred ultimate causations of these features are indicated by sequences of arrows. The key adaptations of the species are judged to be their exclusively arboreal life and their apparent extreme reliance on scavenging. To make the sequences logically complete, the two adaptations are suggested to have been initiated or at least shaped in part by competition from other species of ants specialized for more conventional modes of existence.

The preferred nest sites in dead twigs and branches are exceptionally dry. The *Zacryptocerus* colonies live in cavities that are consistently drier than the nest chambers of ground-dwelling ants, including many species that nest in desert soil. It seems probable that at least two peculiarities, the large size of the eggs and the partial consumption of infrabuccal pellets by the workers, are techniques to reduce water loss.

The 'turtle' defence strategy, which so markedly affects the anatomy of the ants as well as other aspects of their behaviour, is an efficient adaptation in two respects. First, the mandibles of a scavenger species, as opposed to a predaceous one, are likely to be blunt and short, rendering them less effective in defence. Those of *Zacryptocerus varians* have evolved to an extreme in this direction, so that when attacking an intruder the workers are able to do little more than seize a narrow appendage and hang on. As an alternative defence method the species has developed a squat body form with short, robust appendages. When workers are unable to escape more formidable enemies by running and hiding in the many crevices of the plants on which they forage, they can often



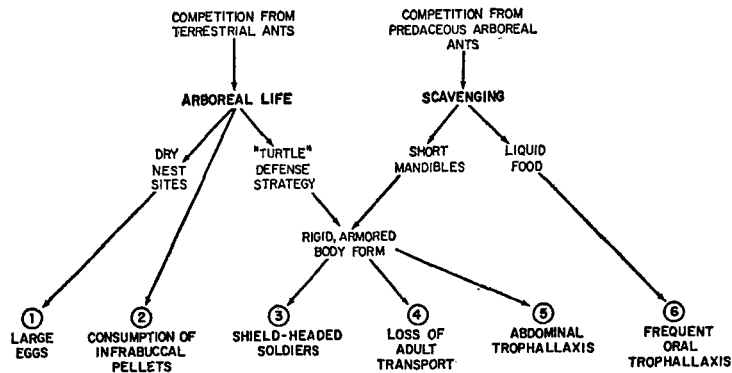


Fig. 2. The postulated relation between the primary ecological adaptation of *Zacryptocerus varians* and its most distinctive social traits.

avoid harm by crouching low and using the flanges and spines arrayed over the top of their bodies as a shield. The antennae are withdrawn into deep scrobes lining the sides of the head. The turtle-like anatomy appears to have evolved in conjunction with at least two other features. The soldier caste has a shield-shaped head which it employs much like the blade of a bulldozer. Lacking long, sharp mandibles, it cannot cut or puncture the bodies of enemies in the manner of the soldier caste of most ant species. And because of its rigid body form, it cannot bring its sting or abdominal glands into easy play. The armoured body form also has the consequence of preventing self-grooming of the abdominal tip. As suggested earlier, the strange mode of abdominal trophallaxis practised by *Z. varians* may be a compensation for this incapacity. The short mandibles and rigid body of the minor worker might also explain why adult transport has never been observed in the species.

Finally, the heavy reliance on scavenging, entailing the consumption of large quantities of liquid and semiliquid food, is a concomitant of the virtual failure of the workers to handle solid food collected outside the nest or to feed solid particles directly to the larvae. This specialization explains the high state of oral trophallaxis observed within the *Z. varians* colony.

The ecological explanations offered here are evolutionary hypotheses based upon intuitively judged correlations. They were derived by the comparison of *Z. varians* with other ant species, so that peculiarities in ecology and behaviour could be identified and linked with one another in a logical manner. The testing of this scheme

awaits further correlations among other species of arboreal and non-arboreal ants, especially within and around the tribes Cephalotini, Cataulacini and Meranoplini, some of whose members resemble *Zacryptocerus* in details of anatomy and ecology. Among the cephalotines the primitive and little-known genus *Procrypto-cerus* seems the most promising. These ants are in some respects intermediate in morphology between more typical myrmicine ants and the most advanced members of the Cephalotini, including *Zacryptocerus*. Whether they are also intermediate in ecology and behaviour is the key question.

#### Acknowledgments

I am grateful to Bert Hölldobler and Robert E. Silberglied for supplying colonies of *Z. varians*, to Professor Hölldobler and Mary Corn for reading the manuscript, and to Robert M. Fagen for calculating the estimated repertory size. The research was supported by National Science Foundation Grant No. GB 40247.

#### REFERENCES

- Coyle, F. A. (1966). Defensive behavior and associated morphological features in three species of the ant genus *Paracryptocerus*. *Insectes Soc.*, **13**, 93–104.
- Creighton, W. S. (1963). Further studies on the habits of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). *Psyche, Cambridge*, **70**, 133–143.
- Creighton, W. S. (1967). Studies on the free colonies of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). *Psyche, Cambridge*, **74**, 34–41.
- Creighton, W. S. & Gregg, R. E. (1954). Studies on the habits and distribution of *Cryptocerus texanus* Santschi (Hymenoptera: Formicidae). *Psyche, Cambridge*, **61**, 41–57.
- Creighton, W. S. & Nutting, W. L. (1965). The habits and distribution of *Cryptocerus rohweri* Wheeler (Hymenoptera: Formicidae). *Psyche, Cambridge*, **72**, 59–64.

- Fagen, R. M. (1974). Theoretical bases for the evolution of play in animals. Ph.D. thesis, Division of Engineering and Applied Physics, Harvard University. (See Chapter 8, pp. 1-44).
- Freeland, J. (1958). Biological and social patterns in the Australian bulldog ants of the genus *Myrmecia*. *Aust. J. Zool.*, **6**, 1-18.
- Hölldobler, B. (1976). Communication in social Hymenoptera. In: *How Animals Communicate* (Ed. by T. Sebeok). Bloomington, Indiana: Indiana University Press. (In press.)
- Kempf, W. W. (1951). A taxonomic study on the ant tribe Cephalotini (Hymenoptera: Formicidae). *Rev. Entomol., Rio de Janeiro*, **22**, 1-244.
- Kempf, W. W. (1958). New studies of the ant tribe Cephalotini (Hym. Formicidae). *Studia Entomol. (Rio de Janeiro)*, **1**, 1-168.
- Kempf, W. W. (1963). Nota sinonimica acerca de formigas da tribo Cephalotini (Hymenoptera: Formicidae). *Rev. Brasil. Biol. (Rio de Janeiro)*, **23**, 435-438.
- Kempf, W. W. (1964). Additions to the knowledge of the cephalotine ants (Hymenoptera: Formicidae). *Papéis Avulsos Dept. Zool. São Paulo*, **16**, 243-255.
- Kempf, W. W. (1973). A new *Zacryptocerus* from Brazil, with the remarks on the generic classification of the tribe Cephalotini (Hymenoptera: Formicidae). *Studia Entomol. (Rio de Janeiro)*, **16**, 449-462.
- Michener, C. D. (1973). Size and form of eggs of allopapine bees. *J. Entomol. Soc. Sth. Africa*, **36**, 281-285.
- Torossian, C. (1959). Les échanges trophallactiques proctodéaux chez la fourmi *Dolichoderus quadripunctatus* (Hyménoptère-Formicoidea). *Insectes Soc.*, **6**, 369-374.
- Wheeler, W. M. & Bailey, I. W. (1920). The feeding habits of pseudomyrmine and other ants. *Trans. Am. Phil. Soc.*, n.s. **22**, 235-279.
- Wilson, E. O. (1962). Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bull. Mus. comp. Zool. Harv.*, **127**, 403-422.
- Wilson, E. O. (1971). *The Insect Societies*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Wilson, E. O. (1974). The soldier of the ant *Camponotus (Colobopsis) fraxinicola* as a trophic caste. *Psyche, Cambridge*, **81**, 182-188.
- Wilson, E. O. (1975). *Lepotothorax duloticus* and the beginnings of slavery in ants. *Evolution*, **29**, 108-119.
- Wilson, E. O. & Fagen, R. M. (1974). On the estimation of total behavioral repertoires in ants. *J. New York Entomol. Soc.*, **82**, 106-112.

(Received 13 January 1975; revised 5 May 1975;  
MS. number: A1655)